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RETINAL REFLEXES OF NARCOTIZED ANIMALS TO SUDDEN CHANGES OF INTENSITY OF ILLUMINATION.

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In March last, Cameron and Sedziak, working in Winnipeg, published a note[1] describing a peculiar reaction of the frog (*R. pipiens* from Illinois), narcotized with benzene, to sudden changes of illumination, a reaction noted incidentally in rehearsing a class experiment on the relative pharmacological effects of different hydrocarbons.

"Injection of 0.5 c.c. of pure benzene into the anterior lymph sac of a frog weighing about fifty grams produces distinct effects within a few minutes. The eyes close, movements become sluggish, when turned over the animal recovers its normal position with difficulty, and in most cases can no longer do so after ten minutes. The body often becomes characteristically arched. The usual reflexes gradually disappear. Breathing ceases. With the gradual disappearance of the conjunctival reflex the eye opens, the nictitating membrane is usually drawn down, and the 'retinal' reflex can be observed. Initially it would appear to be evoked by any rapid change in intensity of illumination. When the hand is passed suddenly between the frog's eye and the source of light, within one or two seconds the head is moved, and usually the hind limbs also. When a bright light (electric light at a distance of one foot) is suddenly switched on, the response follows. On switching the light off the response is more marked. Direction of light to and from the pupil only, the rest of the head being screened from light changes, evokes the response. Gradually the response to sudden increase of illumination ceases. The response to sudden decrease

of illumination persists much longer. Cessation of stimulus therefore appears to be more powerful than application of stimulus. Ether anæsthesia abolishes the response to increase of illumination first.

"The maximum effect is reached at from twenty to twenty-five minutes after injection, and the reflex disappears in another twenty to sixty minutes, or occasionally after even a longer interval. Quality of light does not affect the result; both red and blue light evoke the reflex. Intensity of light appears to be the governing factor. A retina fatigued by the shining of a strong light upon it for some minutes does not call forth such an active response on switching off the light. There may be no movement, but after a minute or two the response can be again elicited by further light stimulation. The degree of response varies in different animals from a slight head movement to such vigorous movements of the hind limbs as would be excited by a strong electric current applied externally. After the reflex has disappeared electrical stimulation still produces active muscular responses. . . . The optimum dose of benzene appears to be 1.2 per cent. of the body weight. Two per cent. induces convulsions and death rapidly, and the retinal reflex can not be observed, while 0.7 per cent. may not produce any definite effect. . . . Similar changes have been observed with toluene, and to a less extent with phenol. Chlorbenzene and brombenzene give the reflex when injected in somewhat larger doses. The reflex could not be detected after injection of similar doses of xylene, aniline, nitrobenzene, benzyl alcohol, and pyridine."

At the same time Fröhlich and Kreidl published an account[2] of similar observations on the prawn *Palæmon squilla* F. found under stones at low tide. These observations were carried out on the island of Brioni in the Adriatic, and initially were accidentally made during experiments to determine the action of certain drugs on the heat-narcosis of these prawns. Fröhlich and Kreidl found that a similar reaction to illumination changes develops in these animals when immersed in sea-water containing camphor or phenol. A small arc-light was used for illumination. Thus for camphor:

"Immersion in camphor sea-water solution of concentration 1 : 16000 is fatal to *Palæmon* in from five to fifteen minutes. The

toxic effects appear as twitches of the limbs and claws, convulsive strokes of the tail, while, when a number of animals are placed in the same vessel, they cling to each other in an entangled mass which is not easily separable. The convulsions are of such a nature that the animal clings fast to the nearest object, especially to the soft legs of its neighbors. If at this stage of camphor poisoning before permanent paralysis sets in the animal is removed rapidly to sea-water, the toxic effects just described—muscular twitchings and convulsions—disappear rapidly. *There remains, however, a pronounced photic over-excitability,* which is manifested by the animal making *very pronounced springs* when the light intensity is rapidly increased, *but on removal of the strong light, violent springs and tail-strokes. . . . The rise of reflex-excitability on sudden lessening of light-intensity was constant at the same phase of camphor action. . . .* There was no trace of a reflex increase for tactile stimuli, neither by shaking the vessel, nor by gently touching the head or tail."

Similar results were obtained with phenol in sea-water. A concentration of 1 : 2000 was rapidly fatal, one of 1 : 5000 less rapid in action. Removal to sea-water before complete paralysis permitted the same light reactions to be observed, especially that of removal of light. Strychnine, ammonia, and caffeine did not produce the effect.

Fröhlich and Kreidl point out that under natural conditions various animals react more strongly to shadow than to sudden increase of light intensity. Sarasin in 1887 (*Diadema setosum*)[3] and Uexküll in 1896 (*Centrospinus longispinus*)[4] noted that sea-urchins react to shadow but not to light with movements of the spines, and Hess, in 1915,[5] showed that shadow, but not light increase, produces in them rotating movements of certain flask-shaped structures. Franz (1919)[6] has shown the existence of the shadow reactions in snails. Fröhlich and Kreidl consider that the reaction is protective, and that the difference in the "cerebrally" poisoned and centrally irritable *Palæmon* is only quantitative.

In the experiments now to be described we have endeavored to link up the experiments of these workers with those of Cameron and Sedziak, since the phenomenon is obviously the same in the two series.

Experimental Results.

Experiments have been carried out with benzene, phenol, camphor, and menthol. The benzene used was Merck's "highest purity, crystallizable," the phenol and menthol were commercial preparations. Two preparations of camphor were used: one, a Japanese commercial product, M. P. 174° C.; the second, a thrice resublimed preparation with M. P. 173.5° C. The latter gave somewhat more pronounced results. The menthol and camphor solutions were made by dissolving them in about twice their weight of absolute alcohol, and adding this to sea-water. The drug was precipitated in finely divided form and saturation of the sea-water followed rapidly. Tests with the same amount of alcohol in sea-water gave completely negative results. Various strengths of solution were used. These are indicated in brackets. The changes in illumination were effected by means of an acetylene lamp, which was suddenly shone on the vessel containing the animals under observation, and suddenly screened or removed. In the following account "light" signifies a sudden marked increase of illumination, "darkness" a sudden marked decrease. The animals were contained in large beakers, and sometimes in large porcelain evaporating basins.

A large number of marine species have been tested. These were selected largely with an idea of ascertaining in how wide a distribution of species the reflex could be obtained. Our choice was to some extent restricted, however, since it was limited to the species easily available.

The experiments are arranged in the order of the species tested.

1. *Cœlenterata. Hydromedusa. Gonionemus vertens.*—A common jelly-fish found amongst the eel-grass (*Zostera marina*) near the station at low tide.

Benzene (1 : 2000) produced no effect. The animal contracted normally after 15 hours. Light variations produced no discernible effect.

Camphor (resublimed, 1 : 16000) produced no effect. The animal was quiescent after two or three hours, but still contracted when touched after 18 hours. Light variations produced no discernible effects.

2. *Echinodermata. Echinoidea. Strongylocentrotus drobachiensis.*—Sea-urchins found on the under surface of the float on the station wharf.

Benzene (1 : 2000) produced an immediate immobility, and light changes ceased to produce any movement of spines. The animal was completely narcotized in six minutes.

Camphor (resublimed, 1 : 16000) produced the same result, and was fatal in less than eleven minutes.

Menthol (half-saturated) produced quiescence in three minutes. Light changes produced no discernible results.

3*a*. *Arthropoda. Crustacea. Decapoda.*

(*A*) *Hemigrapsus nudus.*—A shore crab found plentifully between tides under rocks at the station. When specimens were placed in sea-water under the experimental conditions, "darkness" produced a sudden stoppage of movement, and an occasional "flick," very slight.

Benzene (1 : 1500) produced narcosis in one or two minutes. Before this was complete the crab reacted to "light" by general activity—movement of chelæ and legs, and sometimes of the eye-stalk. "Darkness" produced no effect.

Benzene (1 : 3000). Two animals gave a "darkness" response, definite, but not much greater than normal, after one minute. After five minutes even touching them produced no response, and after ten minutes narcosis was complete.

Phenol (1 : 2000) was fatal to these crabs in from 30 to 40 minutes. Some minutes previously to death both "light" and "darkness" produced marked reflexes.

Camphor (1 : 16000) produced no effect. The crabs were normal after 6 hours' immersion. The resublimed camphor (1 : 16000) produced in a somewhat small specimen (7 grams) a "darkness" response in 10 minutes, and in a larger one in 40 minutes. In 45 minutes both gave marked responses, which continued for some time. After 15 hours' immersion slight responses could be elicited. It was doubtful that these were greater than normal. The animals were otherwise normal at that period.

(*B*) *Epialtus productus.*—A "kelp crab," a somewhat larger species, found amongst eel-grass near the station at low tide.

Benzene (1 : 2000). A large specimen immersed in this solu-

tion became more active. After 45 minutes activity had nearly ceased. The "darkness" reflex was present, but not marked. It was shown by sudden spasmodic movements of legs and chelæ. After a further 15 minutes a "light" reaction was doubtfully present; the "darkness" reaction was marked. The latter slowly decreased. After 70 minutes' immersion the crab scarcely responded to any stimulus. It was then removed to fresh sea-water and slowly recovered.

Camphor (1:16000). A smaller specimen showed a marked "darkness" reaction seven minutes after immersion. There was a general "flick" of legs and chelæ, but no coördination. "Light" produced no effect. After nine minutes' immersion the reaction was no longer given; the animal scarcely responded to any stimulus. Transferred to fresh sea-water, it did not recover.

Menthol (saturated solution). A similarly sized small specimen showed the "darkness" reaction after 12 minutes' immersion. The "light" response became evident after 22 minutes, and after 30 minutes both "light" and "darkness" responses were distinct. The animal commenced to struggle violently, shed both chelæ and three legs, and thereafter became scarcely responsive to any stimulus and (35 minutes) was evidently moribund.

(*C*) *Cancer productus.*—A fairly large crab found on the sea-bottom near the station wharf. Specimens placed in fresh sea-water under experimental conditions gave no noticeable response to changes of illumination. "Darkness" produced very occasionally slight twitches, shown chiefly by movements of the claws.

Benzene (1:1500). A medium-sized specimen (93 grams) was immersed. In six minutes a "darkness" reaction was evident. In 18 minutes both "light" and "darkness" responses were marked. The response consisted of spasmodic contractions of the legs and claws, so that the whole crab was raised. When placed on its back and tested, all the limbs suddenly contracted. The third maxilliped shut and the abdomen was brought up tightly against the carapace. After 32 minutes "light" and "darkness" responses were still evident, but slight, and on touching the animal little response was evoked. After 38 minutes the animal was apparently dead. It was removed to fresh sea-water, but did not recover.

Phenol (1 : 2000) was tested on a larger specimen weighing 140 grams. The "darkness" response was first noted after five minutes. After 18 minutes the "light" response was present, and the "darkness" response was much more marked. A second immediate "light" response produced a much greater reaction. The animal was by no means narcotized at this stage, tapping and touching still yielding marked responses. After 45 minutes the "darkness" response was still noticeable, but at the end of 70 minutes scarcely any responses were obtainable. The animal was removed to fresh sea-water, but did not recover.

Camphor (1 : 16000) was tested on a crab weighing 96 grams. The "darkness" response was just observable after 22 minutes. After 50 minutes "light" produced a response, "darkness" a much more marked one. After 77 minutes the animal remained on its back. It reacted strongly to both "light" and "darkness." The reaction was still evident after four hours and the animal was then by no means completely narcotized. After seven and one half hours only feeble responses were given and the animal was evidently moribund.

Menthol (saturated solution) was tested on a crab weighing 75 grams. The animal became very active immediately after immersion. "Darkness" produced a slight response after three minutes. After 10 minutes the reaction was very evident, but only with distinct pauses between each test. It continued, with gradual lessening, for three hours. No definite "light" response could be elicited. The animal appeared normal throughout with the exception of this response.

(*D*) *Calianassa californiensis.*—A large burrowing sand-shrimp found at low tide at Lock Bay on Gabriola Island, about three miles from the station.

Benzene (1 : 1500) produced a marked effect in 20 minutes. The shrimps remained on their backs with only occasional tail-twitches. After 45 minutes' immersion they were removed to fresh sea-water. They slowly recovered. During this period "light" produced definite tail movements. "Darkness" did not produce a definite effect.

Phenol (1 : 2000) produced complete narcosis in 17 minutes. The animals were transferred to fresh sea-water. Neither during

narcosis nor during recovery were any "light" or "darkness" reactions observable.

Camphor (1:16000) produced no effects. After four hours' immersion the animals were quite normal.

(*E*) *Spirontocaris paludicola.*—A small shrimp found amongst the eel-grass at low tide.

Camphor (resublimed, 1:16000) produced narcosis in 12 minutes. The animals did not curl up. Transferred to sea-water, they slowly recovered. During this period a "light" reaction was doubtfully present. No "darkness" reaction was observed. A somewhat larger specimen was narcotized within one minute. During recovery after transference to fresh sea-water similar doubtful effects were obtained.

(*F*) *Hippolyte californiensis.*—Small shrimps found amongst eel-grass.

Benzene (1:1500) caused at first activity. The animals became sluggish and showed some tendency to cling together in chains (apparently a similar effect to that observed by Fröhlich and Kreidl with prawns in camphor). During this period no "light" and "darkness" responses were observed. After 20 minutes the animals were transferred to fresh sea-water. Within two or three minutes "light" produced a definite response, and "darkness" a much more marked one. These consisted of slight twitches throughout the body of the animal, jerks of antennæ and legs sometimes sufficient to move the animal its own length from its original position. Tapping or touching the animal at this period produced no effect. A second experiment with (1:2000) benzene produced almost complete narcosis in 14 minutes, and, after transference to fresh sea-water, positive "light" and "darkness" responses in four minutes.

Phenol (1:2000 and 1:4000) was fatal within one minute. Phenol (1:10000) was fatal in two or three minutes. No responses to "light" or "darkness" were observed.

Camphor (resublimed, 1:16000) produced a marked action. At first the animals gave marked springs, then curled up. During this period "light" and "darkness" reactions were absent. After four or five minutes the animals were transferred to sea-water. They immediately commenced to relax. Several gave distinct re-

sponses to "darkness" similar to those described for benzene. The reactions to "light" were less certain. Some animals were killed by five minutes' immersion.

Menthol (half-saturated solution) caused almost complete narcosis in 14 minutes, during which time there was some tendency to curl up and to cling together. Transferred to fresh sea-water, during the recovery period the animals appeared to give some "light" and "darkness" responses, though these were less certain than in benzene, and certainly less great.

3*b*. *Arthropoda. Crustacea. Peracarida.*

Amphipoda.—Camphor (1 : 16000) produced no effect during 14 minutes on some specimens of a species found on eel-grass.

Isopoda. Pentidotea wosnesenskii.—A small isopod found on eel-grass. Normal animals under the conditions of experiment showed little response to "light" and "darkness." Occasional "flicks" backward of head and antennæ occurred, but could not be related to illumination changes.

Benzene (1 : 2000) produced a definite effect in five minutes, the "darkness" response being distinct, that to "light" much less, but still observable. Tapping the vessel or the table on which it was resting produced the same sort of response. The reactions persisted for 30 minutes. They consisted of movements of the antennæ, "kicks" when the animals were on their backs, and, when on their legs, these were extended simultaneously so that the whole animal was lifted, and at the same time the opercula were "flicked." The responses gradually lessened with time. The best were obtained when the animal had been brightly illuminated for one or two minutes, and then the source of bright light suddenly removed. An immersion of from two and one half to three hours proved fatal.

Phenol (1 : 2000) gave similar "darkness" and tap responses after 20 minutes. These were not so marked as with benzene, and "light" responses were not observed.

Camphor (resublimed, 1 : 16000) produced no effect in eight hours, the animals appearing completely normal. A saturated solution produced no effect.

Menthol (half-saturated solution) produced definite "light" and "darkness" responses within 10 minutes. The animals were not

so narcotized as with benzene. The response was evident as a flick back of head and antennæ. The animals ceased to respond after 90 minutes' immersion. They were transferred to fresh sea-water and during recovery gave similar but slighter responses to "darkness."

4. *Mollusca. Nudibranchia. Hermissenda opalescens.*—A specimen was found on eel-grass.

Camphor (resublimed, 1 : 16000) was tested on this specimen. After an hour there was some appearance of a reaction to "light," but none to "darkness." After 11 hours the animal was still just alive.

5*a*. *Vertebrata. Pisces.*

(*A*) *Cottoid* (*sp.*).—Small fish, too young for identification, about one inch long, caught in pools near low-water mark.

Benzene (1 : 1500) was fatal in three minutes. Benzene (1 : 3000) was fatal in less than 13 minutes. No responses to illumination changes could be detected. A (1 : 5000) solution was fatal to some animals in seven minutes. At this period in two cases a definite reaction (flick of body) was obtained with "light," but none was observed with "darkness."

Phenol (1 : 2000) was fatal to two of three animals in two minutes. The third was transferred to fresh sea-water and gave one or two doubtful responses to light changes.

Camphor (resublimed, 1 : 16000) was without effect. The fish were normal after three and one half hours.

(*B*) *Pholis ornatus.*—Blennids caught at low tide amongst the eel-grass.

Benzene (1 : 3000). Two small specimens, about three inches long, were almost narcotized in three minutes. They were transferred to fresh sea-water. No reaction to "light" was observed, but several definite responses to "darkness" were obtained. After 12 minutes both animals were dead.

Phenol (1 : 2000). Two similarly sized specimens were immersed and became narcotized in one minute. No definite light responses were observed. The animals were transferred to fresh sea-water, but did not recover. Two similar specimens were immersed in (1 : 4000) phenol. Definite "light" and "darkness" responses were given within one or two minutes of immersion.

The animals ceased to respond after six minutes, were transferred to fresh sea-water, but did not recover. A large blennid, apparently completely recovered from treatment with camphor, immersed in this solution, gave almost immediately a definite response to "darkness," but none to "light." It ceased to respond after five minutes.

Camphor (resublimed, 1:16000). One large specimen, about five inches long, gave a definite "light" and a more marked "darkness" response after 10 minutes' immersion. These responses consisted of a twitch of the tail and sometimes of the whole body. Tapping the vessel containing the animal induced a similar response. That to "light" ceased first. After 15 minutes' immersion the animal appeared completely unconscious. It was transferred to fresh water and recovered. It gave no definite responses during recovery. A still larger specimen immersed in this solution gave very definite responses within three minutes, those for "darkness" being much more marked. The reflex gradually disappeared. After 13 minutes breathing had stopped, but the "darkness" response could still be elicited. After 20 minutes no responses could be obtained to any stimulus. The animal was returned to fresh sea-water and recovered. Two small specimens which had been kept several hours in the laboratory were narcotized in about 10 minutes. No illumination responses were seen.

(*C*) *Siphostoma griseolineatum*.—A species of pipe-fish about six inches long caught amongst eel-grass at low tide.

Benzene (1:3000). Two animals gave a very positive "darkness" response after eight minutes' immersion. That to "light" was less. The response was indicated by a spasmodic jerk. It could be elicited during an additional 15 minutes. Both animals gave marked responses even after tap and tactile stimuli had ceased to produce much reaction, and after breathing had stopped.

Phenol (1:4000). A specimen, previously treated with camphor, and apparently completely recovered, gave, after 10 minutes' immersion, positive "light" responses and more marked "darkness" responses. A fresh specimen immersed in a (1:5000) solution gave slight responses after 10 minutes' immersion, which were more distinct for "darkness."

Camphor (resublimed, 1:16000). A specimen gave a response

to "darkness" in eight minutes. In 12 minutes it appeared narcotized, was removed to fresh sea-water for five minutes, and then replaced in the camphor solution. Subsequently it gave very marked "darkness" responses and less marked "light" reactions, these continuing during 15 minutes. It was then transferred to fresh sea-water and slowly recovered. No definite responses could be detected during recovery.

Camphor (1 : 16000). A specimen, kept for two and one half hours in the laboratory, was immersed. It appeared completely narcotized within a few minutes. It was transferred to fresh sea-water, and then replaced in the camphor solution. After repeating this procedure again, it gave slight but definite "light" and "darkness" responses.

Menthol (half-saturated solution) produced in two specimens complete paralysis within a few minutes. The animals became absolutely limp, in marked contrast to the action of the other compounds used, which ultimately produced rigidity. They were transferred to fresh sea-water and slowly recovered. No illumination responses could be detected at any period of treatment. A saturated solution produced an immediate "limp" paralysis. A particularly large fish (eight inches long) immersed in a one fifth saturated solution showed no apparent effect of any kind in 45 minutes.

(*D*) *Gasterosteus williamsoni microcephalus.* — Californian stiklebacks, caught when free swimming near the station wharf. Under the conditions of experiment changes in intensity of illumination produced no effect on the normal fish.

Benzene (1 : 1500). Three specimens were tested. One, 24 mm. long, gave distinct positive reaction to "darkness" in four minutes. This consisted of flicks of the tail and forward movements. During constant illumination at this stage the animal was quiescent. After five and one half minutes the animal appeared moribund, and on removal to fresh sea-water it did not recover. "Light" did not produce definite responses at any period. A second animal of similar size was completely narcotized in less than two minutes. Some doubtful "darkness" responses were observed. The third, somewhat larger (33 mm.) and more active, gave "darkness" responses in from four to five minutes after

immersion. After 14 minutes the animal was motionless and had ceased to respond even to direct touch. On removal to fresh sea-water it slowly recovered. During this period "darkness" frequently seemed to produce a backward and upward movement four or five times the length of the fish. This immediately ceased on switching on the light, the animal sinking.

5*b*. *Vertebrata. Amphibia. Rana pipiens.*—The results of Cameron and Sedziak for the frog under the action of benzene and phenol have already been quoted. In order to complete this record, the following experiments were carried out at the University of Manitoba:

Camphor (commercial preparation) was tested in two ways. (*a*) 0.5 c.c. of a 20 per cent. solution in absolute alcohol was injected into the anterior lymph sac of a frog weighing 60 grams. There resulted gradual onset of paralysis, the respiratory movements being the last retained. The animal died in about one and one half hours. Change of illumination produced no effect at any period. Since the immediate result of contact of the solution with body fluid is precipitation of finely divided camphor, with subsequent slow solution, no certain dosage in this experiment could be attempted. In a second frog injected with a smaller dose paralysis intervened sooner, and again no "light" and "darkness" effects could be elicited. (*b*) Two frogs were immersed in water saturated with camphor. There was a much slower onset of paralysis. One was almost completely paralyzed in three hours, the second slightly affected. On removal from water breathing recommenced, but the animals subsequently died. There was no evidence of reaction to light changes at any period.

Discussion of Results.

It is evident that the response of animals under a certain type of narcosis to illumination changes is widespread throughout marine species; this is probably true for land animals also. Our observations have been limited to species in which definite responses could easily be detected. More detailed study would probably reveal minuter changes, which, if employed, would show that the phenomenon is even more general. It is probable also that in certain cases

a greater range of dilutions of the chemical compounds employed would yield more definite results; *e.g.,* our results for certain species of shrimps are inconclusive, and we have been unable to demonstrate "darkness" responses with narcotized sea-urchins, though these have been reported for the normal animal.

In addition to the normal "shadow" responses quoted in the introduction may be mentioned here the well-known reaction of frogs to shadow (immediate diving) and that of cryptobranchiate nudibranchs (retraction of the gill-plumes within the branchial collar). Similarly *Euglena viridis* sinks.

The response itself is obviously adaptive (*i.e.,* of survival value, and so likely to have been accentuated by selection), since under natural conditions a shadow suddenly falling on an animal implies the interposition of a solid object between it and the light—*i.e.,* a probable enemy. It is extremely well developed in the pelagic fishes, as we found to our cost when trying to catch them. This normal response becomes less marked in all animals when examined in the laboratory under experimental conditions.

The peculiarity of the response in the narcotized animal seems to consist in its accentuation, actually, or relatively through the abolition of volitional movements and other reflexes, so that its manifestation can be controlled experimentally.

The reaction is always definitely a reflex, though the animal may be by no means in a condition of complete narcosis. While cessation of a very intense illumination undoubtedly produces greater effects than cessation of a lesser degree of it, the sudden change is the controlling factor, and is quite effective when made from a brilliant to a dull but distinct light. In almost all cases it is necessary to allow the animal to rest in dull light for a minute or two between tests, as after repeated subjection to strong illumination the response ceases. This is obviously connected with fatigue due to photochemical changes of the retinal pigment present alike in vertebrates and arthropods. While undoubtedly the retina is the receptor of the stimulus in animals possessing it, the normal reactions of sea-urchins suggest that their color spots can function in a similar way.

Increase of illumination either produces no effect or one much smaller than a similar decrease. There were one or two excep-

tions to this general rule. Thus *Calianassa,* a burrowing shrimp, gave positive reactions with "light" and none with "darkness." It is interesting to note in passing that certain animals normally living or moving in darkness appear to give such a reversed reaction. The well-known responses of the earthworm and of *Mya arenaria* may be quoted. But the subject can not be pressed further without more experimental evidence.

In a large number of cases the animal also responds to mechanical stimulation such as tapping the table on which the containing vessel rests at a period at which the retinal reflex becomes evident. The type of response is somewhat similar to that evoked by illumination changes and is often not yielded by the conscious animal subjected to the same slight stimulus. It nearly always ceases to produce a response much earlier than the "darkness" stimulus.

The results that we have recorded above have some interest from the pharmacological viewpoint. The action of the drugs employed is by no means similar in higher species (cf. Cushny[7]).

Camphor, in the frog, depresses the brain, and later the spinal cord, the action being a descending paralysis. There is no excitement, the reflexes gradually disappear, and the animal lies completely paralyzed. In mammals convulsions, due to stimulation of the higher areas of the nervous axis, are usually produced, and gradually pass into depression, stupor, collapse, and death from cessation of respiration, the cerebral cortex, medulla, and cord being in turn paralyzed. The terminations of the motor nerves are paralyzed in the frog by large doses (which may account for our failure to elicit the retinal reflex with camphor), but not in mammals. Menthol produces a similar series of phenomena, but there is less tendency to convulsions.

Phenol, in the frog, first causes depression and loss of spontaneous movements, later augmented reflex excitability, and finally tonic convulsions (due to increased irritability of the spinal cord). Complete paralysis of the central nervous system supervenes. Similar symptoms are produced in mammals, but there is often no preliminary stage of depression. The peripheral nerves and muscles are not affected in mammals and scarcely, if at all, in the frog. Benzene is stated to be much less toxic than phenol, though when

inhaled in large quantities it may give rise to similar symptoms. In some animals it produces violent and prolonged convulsions.

The differences of behavior exhibited by frogs and mammals to these drugs are shown by our results for the specific reflex that we have studied to be even greater when the observations are extended to include invertebrates. Although undoubtedly, as Cameron and Sedziak found for frogs, the degree of reaction differs markedly in different animals of the same species, and though our results were in some cases affected by the length of time that the animals were kept in the laboratory before they were tested, yet such marked variations are shown that a distinct idiosyncrasy of different species to the action of certain drugs is indicated. Thus camphor was little or non-toxic and did not reveal the reflex in cottoids and isopods; to the frog it was toxic, but the reflex could not be demonstrated; while with crabs, blennids, and pipe-fish marked responses to illumination changes were obtained with a varying degree of toxicity. Camphor was non-toxic for one species of shrimp, toxic but ineffective for a second, toxic and effective for a third; it gave marked reactions with the prawn employed by Fröhlich and Kreidl.

Quantitative comparison of the different drugs is difficult, not only on account of the different concentrations employed, but chiefly because of our ignorance of the rate of absorption of these drugs by different species and different sized specimens. The results for phenol and benzene can perhaps be contrasted most satisfactorily; it would seem that benzene is slightly less toxic, but it was of all the drugs employed the one most favorable for the production of the retinal reflex. It is to be noted that in at least one species (the isopods examined) for which camphor was non-toxic benzene was distinctly toxic.

It would seem that in most of the species studied benzene produces on the central nervous system an action distinctly comparable to the typical paralyzing action of phenol and camphor, and relatively much greater than that it produces in mammals.

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